

Four new half-and-half mosaic fowls

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INTRODUCTION

Half-and-half mosaics, i.e. genetic chimaeras whose two components comprise, at least approximately, the right and left halves of the body, have been recorded in several species of birds (references in Hollander, 1944). In mammals, on the other hand, they seem to be almost unknown; all the mosaics mentioned by Robinson (1957) are pigmentation mosaics with irregular and relatively small abnormal patches, although Zlotnikoff (1945) has described a human mosaic with a half-and-half arrangement, and it is possible that some of the cases of lateral hermaphroditism in rodents are mosaics (see Glass, 1945).

In the domestic fowl, at least twenty-two half-and-half cases have been recorded (Blyth & Hale, 1953; Jerome & Huntsman, 1959; other references in Cock, 1955); there are besides, a few cases which are probably half-and-half, but where a more restricted type of mosaicism cannot be excluded. In most cases the two sides of the body have differed in size, as well as in one or more such characters as skin colour, plumage pigmentation and structure, and eight of them have had hermaphroditic gonads (right testis, left ovary or ovotestis). Their mode of origin has been a long-standing puzzle. Loss or non-disjunction of a single chromosome at first cleavage has been the favoured explanation for most of them, but it is not universally applicable. Each of the three cases of Greenwood & Blyth (1951) and Blyth (1954) is mosaic for a sex-linked and an autosomal gene; there are also serious, if less obviously decisive, obstacles to applying a single-chromosome explanation to several other cases (Cock, 1955). Alternative explanations which have been proposed for some cases include the involvement of polar bodies (fertilized or unfertilized), or of supernumerary spermatozoa (giving rise to tissues of purely paternal origin), and the maldistribution of two or more chromosomes at first cleavage. The inevitable uncertainties due to incomplete information (e.g. uncertain parentage, lack of suitable marker genes in the parents, absence of a progeny test) are increased by the fact that no one explanation is capable of accounting for all the known cases.

Two of the cases now to be described are of particular interest, since, like those of Greenwood & Blyth, they are mosaic for both sex-linked and autosomal genes. They are, moreover, full brothers, and family information about them is unusually complete; parents, normal siblings and offspring have all been examined. The other two cases are less remarkable and will be described more briefly. All four cases are cross-bred, and all have the Light Sussex as one parental breed, the other breeds involved

being Brown Leghorn, Indian Game (Dark Cornish) and Rhode Island Red. Some preliminary account of the genetics of the breed differences is necessary; the important differences are summarized in Table 1.

The genes affecting skin colour and comb (W and P) are dominants which segregate sharply, but the genetics of the plumage colours and patterns is rather more complex. The black-red plumage of the Brown Leghorn, with its strong sexual dimorphism, may, following Hutt (1949), be taken as a convenient 'wild' or standard type. The plumage of the Light Sussex differs from this in two respects: (i) black pigment is restricted to parts of the wings, neck and tail (the so-called Columbian pattern); (ii) the remainder of the plumage is white, instead of varying shades of brown, red or yellow. The second difference is due to the sex-linked dominant S

Table 1

	Brown Leghorn	Rhode Island Red	Indian Game	Light Sussex
Comb type	pp	pp	PP	pp
Skin colour	$w w$	$w w$	$w w$	$W W$
Plumage colour	$s s$	$s s$	$s s$	$S S$
Plumage pattern (extent of black)	$co co$	$Co Co$	$co co$ (modified)	$Co Co$
Ear-lobe colour	white	red	red	red
Body weight ($\delta\delta$) g.	2300	3400	3800	3400

p = single
 w = yellow
 s = gold
 co = Brown Leghorn pattern

P = pea autosomal
 W = white autosomal
 S = silver (white) sex-linked (δ homogametic)
 Co = Columbian restriction of black autosomal

Ear-lobe colour shows irregular 'blending' inheritance. The figures for body weight are from the standard weights given by Jull (1940, Table 2); they are intended merely to indicate the order of magnitude of size differences, since there is a great amount of within-breed variation.

(silver), which inhibits most brown, red and yellow pigments, but is without effect on the distribution of black. There are some brownish pigments which are not inhibited by S (the salmon breast of the Brown Leghorn female is the most clear-cut example) but there is usually no difficulty in diagnosing S either in chick downs or in adult plumage.

Columbian restriction of black has been ascribed (Smyth & Bohren, 1949; Kimball, 1954) to an allele (e^c) of self-black (E), recessive to E , but dominant to a third allele (e^+) present in Brown Leghorns. Critical evidence for or against allelism is lacking, partly because Columbian does not, or at least does not always, segregate sharply from Brown Leghorn pattern. This is clear, both from past experience (Pease & Cock, 1951) and from the breeding tests reported later in this paper. F_1 's usually approximate to Columbian pattern, with black slightly more extensive than in purebred Columbians, but a wide range of types occurs in segregating generations,

with the extent of black varying, often without any clear discontinuity, from typical Columbian, through intermediate grades to Brown Leghorn pattern and sometimes beyond. Similar difficulties arise if chick down instead of adult plumage is taken as the criterion. Columbian breeds have a plain-coloured down (buff or reddish-brown in the absence of *S*, otherwise white) with black pigment confined to the bases of the growing wing-quills, whereas the Brown Leghorn has a broad dark dorsal stripe, with additional lateral stripes on the hips and through the eyes. F_1 downs are plain (although a black spot on the head, or traces of black on the back often occur, usually in females), but in segregating generations all grades appear, from plain downs, through various degrees of 'reduced' and narrow stripes to typical Brown Leghorn downs. The striping may be distinct or more or less blurred, and downs with a mottled instead of a striped pattern occur. There is, moreover, no very close relationship between chick down and adult plumage; the plain downs tend to grow into Columbian, and the broader stripes into Brown Leghorn pattern, but there are exceptions in both directions (cf. Pease and Cock, 1951).

The assumption of a single major autosomal gene (probably imperfect in dominance) for Columbian restriction, with modifying factors blurring the segregation, does seem to be justified. The symbol *Co* is used here without prejudice to the question of allelism with *E*, which is irrelevant to present purposes. There is an admitted element of arbitrariness in classifying progeny for *Co*; classification has been based on adult plumage rather than on chick down.

The above account omits several minor variations in plumage pattern, whose genetic basis is uncertain. These include differences in the intensity and quality of brown-red-yellow colours, e.g. the dark red-brown ground colour of Rhode Island Reds, contrasted with the paler, more yellow colour of F_1 females from Brown Leghorn ♂ × Light Sussex ♀. Again, some female *S*-segregants have the Brown Leghorn distribution of black, but a white instead of a salmon breast; these have been taken to be *co*-types. There is probably a corresponding group among *S*-segregants, with the breast a golden instead of a salmon colour, but the corresponding types in males are presumably indistinguishable, since the breast in *co*-males is black. The pattern of the Indian Game has been ascribed to yet another allele at the *E*-locus, but for present purposes it suffices to regard it as a modified *co*-type.

Cases F1218 and E2785

These are both fully fertile males, with normal male secondary sexual characters and behaviour; normal male genitalia were found at autopsy. They were produced in the course of an experiment on crossing the Brown Leghorn and Light Sussex breeds, carried out by Mr R. W. Hale at the Agricultural Research Institute of Northern Ireland, Hillsborough, County Down. The pen from which they were bred contained females of both breeds, and two males, one of each breed, were placed in the pen on alternate weeks. Progeny of four types (the two pure breeds and their reciprocal F_1 's) were thus produced from the same pen. Chicks were pedigreed to individual dams by trap-nesting; in female chicks paternity could be determined from down colour. Sex, when not evident from down colour, was

established by examination of the vent, and all males were normally discarded at hatching time. The dam of both the mosaics is a typical Light Sussex (D229); it is practically certain that they were sired by the Brown Leghorn (D832). Although it is formally possible that the Light Sussex male (D222) was in some way involved in paternity, this seems extremely unlikely, as all deviations in the mosaics from a normal F_1 male phenotype are in a Brown Leghorn direction. However, it was thought advisable to progeny test the Light Sussex male as well as the mosaics and their parents, and Mr Hale very kindly sent these five birds to Edinburgh in August 1958.

F1218

Hatched: 19 March 1958. Killed in emaciated condition 6 February 1959. Post-mortem examination revealed no abnormalities other than a mild nephritis.

Down colour: buff, i.e. like a normal F_1 female. It was in fact taken to be such until the male sex and mosaic skin colour were noticed at 8 weeks of age.

Body weight: 3020 g. (4 September 1958).

Skin colour: left shank rich yellow (*w*); right shank white (*W*). The effect of *W* on the colour of the body skin is slight, but there is a median line of division between white and yellow skin discernible along the keel of the sternum.

Adult plumage: the superficial appearance is closely similar to that of a normal Brown Leghorn male, and there is no perceptible difference between right and left sides. Closer examination reveals a departure from normal Brown Leghorn colouration. This consists in a substitution of white for gold or red-brown in the non-black parts of many of the feathers of the neck and saddle, and of all the wing secondaries. All the feathers so affected have gold colouration at the distal end, which fades gradually into white proximally. There is also a little scattered white in the wing coverts. The white could be regarded either as indicating the presence of silver (*S*) in parts of the plumage, or as merely a somewhat atypical expression of gold (*s*). The symmetrical distribution of white, its confinement to the proximal parts of feathers, and the absence of an abrupt boundary between white and gold within single feathers, all favour the latter possibility. The bulk of the plumage is undoubtedly gold, but the possibility that some small patches of silver are present cannot be ruled out.

Ear-lobes: mainly white, with a slight mottling of red on both sides. (This mottling is characteristic of F_1 's, although the relative amounts of white and red vary widely. A little red mottling is sometimes found in pure Brown Leghorns, and is in fact present in D832.)

Skeletal size: the left side is consistently smaller than the right. The average difference in length of the paired bones amounts to 4–5% (Table 2), and the bones of the left side show a corresponding reduction in thickness. Among median bones the asymmetry is less evident. The skull and sternum are both slightly asymmetrical, but none of the vertebrae shows significant asymmetry, and, apart from a slightly shorter ilium on the left, the synsacral complex is remarkably straight and symmetrical.

Table 2. Bone lengths in cm.

	F1218			E2785			Cl			Br		
	R	L	$\frac{R-L}{R}\%$	L	R	$\frac{L-R}{L}\%$	L	R	$\frac{L-R}{L}\%$	L	R	$\frac{L-R}{L}\%$
Femur	11.1	10.6	4.5	11.4	10.6	6.5	10.1	8.8	13	10.2	9.9	3
Tibiotarsus	16.4	15.3	6.5	16.8	15.4	8.5	14.8	14.1	5	14.9	14.6	2
Tarsometatarsus	11.2	10.7	5	11.2	10.2	9.5	10.1	9.9	2	10.1	10.0	1.5
Humerus	9.7	9.5	3	9.9	9.2	7.5	9.0	8.9	1	8.9	8.9	1
Radius	9.0	8.7	4	8.9	8.5	5	8.0	—	—	7.8	7.7	0.5
Ulna	9.9	9.5	4	9.9	9.4	5	8.8	—	—	8.8	8.7	1
Carpometacarpus	5.4	5.3	3	5.4	5.2	5	4.7	4.6	1	4.9	4.8	2
Coracoid	7.5	7.0	7	7.6	7.0	7.5	7.0	6.8	2	6.8	6.7	0.5
Scapula	10.0	9.9	1	10.1	9.3	7.5	—	—	—	—	—	—
Clavicles (excl. hypocleidium)	6.0	5.7	4.5	5.9	5.3	10.5	5.8	5.6	2.5	—	—	—
Ilium	12.5	12.1	3	12.1	10.8	10.5	—	—	—	—	—	—

Gaps in the entries under Cl and Br are due to broken bones; these two skeletons were very fragile. Lengths are given here to the nearest 0.1 cm., but were in fact measured to 0.01 cm. Differences are given to the nearest 0.5%.

E2785

Hatched: 12 March 1958. Died suddenly, 24 April 1959; nephritis was diagnosed.

Down colour: buff, with one white wing.

Body weight: 2900 g. (4 September 1958).

Skin colour: left shank entirely white, right shank pale yellow, with a streak of white running down the back and along one of the toes. In the body skin there is a median line of yellow/white demarcation discernible below the cloaca, but not elsewhere.

Adult plumage: there is a very evident asymmetry in both colour and pattern (Plate I, Figs. 1 and 2). On the ventral side, the division is clear-cut and median, but dorsally it is irregular. The type of the right side extends onto the left of the head, whereas that of the left covers the greater part of both sides of neck and saddle hackles. With this proviso, the two types are as follows. The right side is basically Brown Leghorn type, but, as in F1218, there are minor departures from true Brown Leghorn pattern. The outer edges of the wing-flights are predominantly white, but some have small smudges of gold near the tip, and one primary has a completely gold edge. Analogous whitening may well occur in some of the neck and saddle feathers too; the irregular demarcation between the two types makes certainty about this impossible. Many of the feathers of the ventral plumage and leg (which would be solid black in a normal Brown Leghorn male) have a little brown and/or white mottling near the tip. The plumage of the left side differs in two respects: it is undoubtedly silver (*S*), and it shows a degree of restriction of black intermediate between a typical F_1 and a Brown Leghorn. The surface colour of the breast, ventral abdomen and leg is an irregular mixture of black and white in about equal amounts.

Ear-lobes: predominantly white, with some red mottling on both sides.

Skeletal size: asymmetry is rather more extreme than in F1218, and it is the right side which is smaller (Table 2). The bones of the left side are distinctly thicker as well as longer. The median bones show a more consistent asymmetry than those of F1218. The skull and sternum are both markedly asymmetrical, as are the cervical vertebrae, particularly the more anterior ones. In the thoracic and synsacral regions, the vertebral column has been distorted into a \perp -shape, so that the 6th and 7th thoracic vertebrae (the 7th being the 1st vertebra of the synsacrum) run practically transversely, with their anterior ends towards the right. This, together with the unequal length of the legs, produced a very clumsy stance and gait. At post-mortem examination, the left lobes of the liver were found to be much larger than the right lobes.

Breeding tests

The following test matings were carried out by artificial insemination at Edinburgh in November 1958–January 1959. Apart from the fact that F1218 became obviously unwell during this period, and then yielded little or no semen, fertility and hatchability were satisfactory.

(1) The Brown Leghorn male D832 was mated to the Light Sussex dam D229. Thirty-eight offspring (17 ♀♀ : 21 ♂♂) survived to the eighteenth day of incubation



Fig. 1.



Fig. 2.

Ventral (Fig. 1) and dorsal (Fig. 2) views of E2785. Ventrally, the line of demarcation between the two plumage types is median and sharp; the apparent deviation towards the right side posteriorly in Fig. 1 is due to exposure of the grey underfluff in the region between the sternum and the cloaca. The dorsal demarcation line is much more irregular and indistinct. There are patches of gold at the sides of the comb, along the right border of the neck hackles, and in the saddle; the difference between gold and black, like that between white and yellow skin, does not reproduce well in black-and-white.

Table 3

(a) Classification for S and sex; survivors beyond seventeenth day of incubation

		S	s	Total
F1218	♀♀	9	13	22
	♂♂	15	7	22
	Total	24	20	44
	Dead embryos			10
	Rearing losses			3
	Remaining			31
E2785	♀♀	23	24	47
	♂♂	20	17	37
	Unsexed	—	1	1
	Total	43	42	85
	Dead embryos			11
	Rearing losses			12
Remaining			62	

(b) Classification for S, W and sex; survivors beyond 8 weeks

		S W	S w	s W	s w	Total
F1218	♀♀	3	4	3	4	14
	♂♂	3	9	4	1	17
	Total	6	13	7	5	31
	S : s					19 : 12
	W : w					13 : 18
E2785	♀♀	7	9	10	8	34
	♂♂	4	11	6	7	28
	Total	11	20	16	15	62
	S : s					31 : 31
	W : w					27 : 35

(c) Classification for extent of black in plumage; survivors beyond 8 weeks

	Near F ₁ pattern (Co)	Intermediate (Co?)	Near Brown Leghorn pattern (co)	Total
F1218	7	9	15	31
E2785	12	15	35	62

Offspring of F1218 and E2785 mated to Brown Leghorn hens (s, w, co). Most of the rearing losses are due to a power failure affecting the brooders. Segregation of extent of black in plumage shows no significant association with S, W or sex.

or beyond; all males were silver (*S*) and all females gold (*s*). Twenty-seven of these (10 ♀♀ : 17 ♂♂) were reared to 8 weeks or beyond (when reliable diagnosis of skin-colour is first possible); all were white-skinned (*W*). In addition, eight F_1 and two pure Light Sussex females from D229 had been reared at Hillsborough; these again were all normal.

The plumage pattern of the left side of E2785 differs from a normal F_1 in that black pigment is too extensive. As the degree of restriction of black may show some variation in different F_1 families, the normal sibs afford a critical comparison on this point. In all of them (both sexes), black was only slightly more extensive than in pure Light Sussex; there were always some black markings in the saddle, and usually traces of scattered black in the ventral plumage, but the latter were always small in extent. The normal range of variation in this mating is narrow, and the right side of E2785 lies well beyond it.

(2) The Light Sussex male D222 was mated to Brown Leghorn hens from the Poultry Research Centre flock. Seventy-eight offspring (37 ♀♀ : 41 ♂♂) were obtained, all silver (*S*). Of these, forty-seven were reared to 8 weeks or beyond, all being white-skinned (*W*). The extent of black in the plumage was similar to that in the offspring of mating (1), and showed only slight variations. This male is thus homozygous for the breed characters of the Light Sussex, which makes it even more difficult to imagine that he was in any way involved in the paternity of the mosaics.

(3) The two mosaics were each mated to Brown Leghorn hens; the results are summarized in Table 3. The most striking aspect is the clear evidence that F1218 carries *S* and *Co*, despite his being phenotypically *s* and *co* on both sides. There is, in fact, nothing in the results from either mosaic to distinguish them from normal F_1 's. None of the segregation ratios for sex, *W* or *S* departs significantly from 1 : 1. There is no indication of gonadal mosaicism; the *ws* class, which should then be in excess, is actually below expectation in both cases. If, as is probable, the intermediate class in respect of restriction of black is to be regarded as modified *Co*, the segregation ratios for *Co* also approximate to 1 : 1.

Case Cl

This, like the following case (Br), was studied while the writer was on the staff of the Poultry Genetics Unit, School of Agriculture, University of Cambridge, and was sent in by a private breeder. It was received in August 1954, at the age of about 6 months. Information as to parentage is limited to the fact that it derived from a cross of Indian Game and Light Sussex. The breeder stated that it was probably not an F_1 , but rather an F_2 or backcross. Death occurred in June 1956, and autopsy disclosed extensive tumours in the liver, kidneys and mesenteries. Normal male genitalia were found, and the secondary sexual characters were at all times those of a normal male.

Comb type: pea (*P*).

Skin colour: right shank white (*W*), left shank yellow. No difference in the colour of the body skin of the two sides could be detected. The intense reddening of the mid-ventral skin of this bird would obscure a possible line of yellow/white demar-

cation. (Such reddening is common among Indian Game, due to the short and rather sparse plumage, which leaves the mid-ventral skin exposed.)

Adult plumage: silver Columbian type, but black pigment more extensive than in pure Light Sussex. The two sides differ in this respect, black being slightly but definitely more extensive on the right. The difference is noticeable in the wing-flights and in the breast, which is practically pure white on the left, but has irregular black spangling on the right.

Skeletal size: there is a general reduction in size on the left side, but different bones are not equally affected (Table 2). Whereas the bones of the wing show only a slight and barely significant reduction in length of about 1%, the femur is reduced by 13%, although the reduction becomes progressively less in the more distal leg bones. This is not accompanied by any corresponding reduction in thickness; the shafts of the right femur and tibiotarsus are respectively 15% and 8% thicker (absolutely) than those of the left. In contrast to F1218 and E2785, the two sides of the body thus differ markedly in proportions as well as in size. The ratio between the lengths of tarsometatarsus and femur is 1.12 on the right and 0.99 on the left; comparison with Hutt's (1929) mean value of 0.992 (s.d. 0.014) indicates that it is the smaller right side whose proportions are abnormal. The sternum is concave towards the right, and the skull is slightly asymmetrical, but the vertebral column and synsacrum are practically symmetrical.

Breeding test: mated in 1955 with Brown Leghorn hens, he yielded 126 offspring, all silver (*S*). Good 1 : 1 ratios were obtained for comb-type (63*P* : 63*p*), sex (56♀ : 55♂, dead embryos not sexed) and skin colour (52*W* : 50*w*). Approximately one-half of the offspring had Columbian or modified Columbian plumage pattern; the segregation was fairly sharp in males (29*Co* : 20*co*) but very indistinct in females. These results accord with a genotype of *S/S*; *P/p*; *W/w*; *Co/co*, and give no suggestion of gonadal mosaicism.

Attempts were made in 1956 to obtain offspring from the two testes separately, by everting the cloaca during massage and sucking semen into a pipette as it emerged from the genital papilla. Some semen was obtained in this way, but this, like all other semen collected in 1956, proved to be infertile.

In an attempt to detect a possible red-cell mosaicism, the blood of Cl was tested with three lytic sera kindly supplied by Professor P. B. Medawar. These tests yield no evidence of mosaicism, but failure to detect it with these particular sera does not prove it to be absent.

Case Br

This is an F₁ male (Rhode Island Red ♂ × Light Sussex ♀) received in April 1955 at about 14 weeks of age. It appeared from the start a weakly and underdeveloped individual, and died in August of the same year. Autopsy showed extensive ulceration of the inner surface of the crop. The genitalia were very small for a bird of this age (testes 14 mm. long, 6 mm. diameter) but otherwise apparently normal and entirely male. This was rather surprising, as the secondary sexual characters had been predominantly female. Comb and wattles had remained small and there were no signs of spur growth. Inactive testes could easily account for this, but the

plumage structure was predominantly female, although there were some feathers of male or intermediate type among the wing-coverts. Female-type plumage normally develops only in the presence of ovarian hormone or excess thyroid hormone, but since there was no sign of hermaphroditism in the genitalia, it seems that this was probably in some way due to the persistent poor health, and unconnected with the mosaicism. It is not impossible that the bird carried the henny-feathering gene; there is no evidence to refute or support this.

Skin colour: white (*W*) on the right, yellow on the left, with a clear mid-ventral line of demarcation between white and yellow.

Adult plumage: the plumage pattern is that normal for a male of this cross (i.e. Silver Columbian, with scattered splashes of chestnut) and there is no perceptible asymmetry.

Skeletal size: there is a rather slight reduction in size on the left side (Table 2). There is a tendency, as in case Cl, for the femur and tibiotarsus to be more strongly affected than other limb bones, but this is much less marked. Sternum, thoracic vertebrae and synsacrum all show a curvature, concave on the left.

DISCUSSION

There is no compelling reason to regard either Cl or Br as the result of anything more complicated than loss of the *W*-bearing autosome from one nucleus at first cleavage division; the slight difference in plumage pattern in Cl could easily be due to a modifying gene linked with *W*. However, this explanation rests merely on the absence of contradictory evidence, and can be no more than tentative. The abnormal proportions of the smaller side of Cl recall analogous changes in three earlier cases (Cock, 1955) which were also mosaic for *W*. Changes in size and proportions would be a not unexpected consequence of aneuploidy, but it is difficult to see why they should be extreme in some cases, but very slight in others involving the same locus. According to Newcomer (1957) the fowl has only five pairs of autosomes, corresponding with the five known autosomal linkage groups, plus an indefinite number of small 'chromosomoids'. Despite extensive tests (Warren, 1949) no linkage of *W* with any other gene has yet been detected, which suggests that it may be carried by one of the chromosomoids.

Before considering the possible mode of origin of F1218 and E2785 it is necessary to deal with several points which seem to depend on irregularities in the distribution of descendants of the two original cells. Previous cases have shown departures from a strict half-and-half distribution in the melanocytes (see especially Greenwood & Blyth, 1951, and Jerome & Huntsman, 1959) and in the germ-cells (Greenwood & Blyth, 1951; Blyth, 1954); in view of the migratory embryonic history of melanoblasts and of primitive germ-cells this is not surprising. In E2785 the distribution of the melanocytes, although broadly half-and-half, clearly shows some degree of irregularity. In F1218 neither *S* nor *Co* is expressed in the plumage, but both are present in the gonads; the assumption of an extreme degree of irregularity, so that all or most of the melanocytes of both sides are derived from the left half of the early

embryo, seems to be the only way of reconciling these facts. The breeding results of both cases (and of Cl) are most plausibly interpreted as reflecting irregularities in the origin of the germ-cells, the recessive side of the body being represented, if at all, in numbers too small to cause a significant disturbance of segregation ratios. There is also evidence of departures from a strict half-and-half distribution in the skin (the white patch on the right shank of E2785) and in skeletal tissues (the relatively symmetrical vertebrae and synsacrum of F1218).

With these considerations in mind, F1218 and E2785 are more similar than first appearances suggest. Each has one half (the right in F1218, the left in E2785) whose constitution at least approaches that of the normal F_1 , whereas, the other half resembles the paternal Brown Leghorn, both in the reduced size and in the lack of maternal dominants, *S*, *W* and *Co*. Only two types of explanation of this condition seem even remotely possible. The first is that one side of the body is of purely paternal origin, the other side being derived by a normal fertilization process. The paternal side would presumably be diploid; this could result either from a mitosis with the final stages suppressed, or from the fusion of the nuclei of two supernumerary spermatozoa. The second possible explanation is that a normal fertilization has been followed by multiple maldistribution of the chromosomes at first cleavage division; maldistribution is intended to cover such possibilities as elimination of part or whole chromosomes, non-disjunction, translocation, somatic crossing over.

The hypothesis of purely paternal origin is capable of explaining several previous half-and-half fowl mosaics (Cock, 1955), notably the two cases of Greenwood & Blyth (1951), which show important similarities with the present cases. In addition, several pigeons with irregular (i.e. no sign of a half-and-half arrangement) and restricted pigmentation mosaicism (Hollander, 1949) and one irregular mosaic fowl (Cock, 1959) can be explained in a similar way. In the present cases, although the main features are readily accounted for, there are certain obstacles to the acceptance of this hypothesis.

In both cases the smaller side shows deviations of a relatively minor nature from strict Brown Leghorn phenotype in adult plumage pattern; these might perhaps (although not very plausibly) be explained away, e.g. as the result of islands of silver melanocytes. A more serious difficulty is the fact that the down pattern in both cases was the plain buff characteristic of the F_1 female, without the striping of the pure Brown Leghorn. In the case of F1218 this observation was made before the mosaic nature of the bird was recognized, but Mr Hale assures me that the down certainly was of the unstriped F_1 type, and points out that a down of Brown Leghorn type from this dam would immediately have aroused suspicions of a pedigreeing error. (That an unstriped down should be followed by adult plumage close to Brown Leghorn type is not in itself exceptional; several such cases occurred among the progeny—see Introduction.) A further difficulty is that in E2785 the plumage of the left side has much more black than a normal F_1 . Taken singly, any one of these difficulties might be neglected or explained away, but in conjunction they constitute a serious obstacle to the hypothesis of purely paternal origin.

The second type of explanation, that of multiple maldistribution of the chromosomes, demands a remarkable degree of coincidence, particularly in view of the similarities of the two cases. Since *W* and *Co* are not known to be linked, it would seem that at least two autosomes are involved in addition to the X-chromosome, and in E2785 the departure of the right side from normal F₁ phenotype suggests loss from this side of a third autosome carrying a modifier of *Co*. There are serious difficulties in such an explanation, quite apart from questions of coincidence.

(1) Somatic crossing-over is excluded (at least as the sole cause of the mosaicism) by the breeding results; it would require the larger side to be homozygous for *S* and *W*, so that *Sw* and *sW* types should not appear among the progeny. All other forms of maldistribution would lead to aneuploidy on one or both sides, and it is difficult to believe that multiply aneuploid tissue would be viable, even if, as is possible, both *W* and *Co* are carried on the small 'chromosomoids' of Newcomer (1957).

(2) The chromosomal imbalance involved in aneuploidy, even when not so severe as to be lethal, should lead to disturbances in growth, and abnormalities of proportions on the smaller side have in fact been prominent features of several previous cases (including Cl) mosaic for *W*. There is no sign of similar abnormalities in F1218 or E2785; the variation in degree of reduction in length of different limb bones is relatively slight and does not follow a similar pattern in the two birds.

(3) The normal males gonads are not incompatible with the assumption that one side of the body is XX and the other X-, since the breeding results suggest that all or most of the germ-cells are derived from the XX side. However, in several previous cases which appear on other evidence to have been XX/X- mosaics there has been an average difference of 13 to 15% (i.e. the normal ♂ versus ♀ difference) in the length of the limb bones of the two sides (Cock, 1955, Table 6). The corresponding differences in the present cases are considerably less than this (5% in F1218; 7% in E2785), whereas maldistribution of the autosomes should have increased rather than reduced the difference.

The mode of origin of F1218 and E2785 must therefore remain enigmatic; neither of the two types of explanation considered above is convincing, and yet there seems to be no conceivable third alternative. The aura of uncertainty might have been reduced by cytological comparison of somatic tissues from the two sides; this had been intended but was prevented by the premature death of both birds. The occurrence of two cases in the same family is probably not purely coincidental but reflects an underlying predisposition to mosaicism. In the present instance this might be a non-inherited peculiarity of one or other parent, but mosaics which were descended from a mosaic parent or grandparent, indicating a hereditary tendency, have been reported by Crew & Munro (1939) and by Blyth (1954).

SUMMARY

Two mosaic birds are described, from a sex-linked F₁ cross (Rhode Island Red ♂ × Light Sussex ♀). They are sexually normal males and full brothers. Each has the following abnormalities on one side of the body: absence of the maternal dominants *S* (silver, sex-linked), *W* (white skin) and *Co* (Columbian restriction of black), and

reduction in size. In one case all the melanocytes appear to be derived from the smaller side, so that the plumage pattern is identical on the two sides; in the other there is a minor deviation (modified expression of *Co*) from normal F_1 plumage pattern on the larger side. Mated to Brown Leghorn hens, both mosaics bred as normal F_1 males, with no evidence of germinal mosaicism. Over thirty full sibs were all found to be normal.

A purely paternal origin of the smaller side appears to be excluded in both cases by the lack of striping in the down, and by minor deviations from normal Brown Leghorn phenotype in adult plumage pattern. Origin by some kind of maldistribution of chromosomes at first cleavage division would require the X-chromosome and possibly as many as three autosomes to be affected simultaneously.

Two further unrelated crossbred mosaic males are described. Each has yellow skin (*w*) on one side of the body. In one case this is accompanied by a slight difference in plumage pattern, reduction in size and abnormal proportions in the limb bones; in the other merely by a slight reduction in size. Loss or non-disjunction of a single chromosome at first cleavage division is a possible explanation of these.

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